FURTHER NOTES ON THE BEHAVIOR OF GONIONEMUS

MAX MORSE

THE following notes upon the response of this jelly-fish, Gonionemus, to light supplement those published by the writer in the *Journal of Comparative Neurology and Psychology* in 1906 (Vol. 16, p. 450–456). All the experiments to be described were made in a dark-room to which sunlight was admitted by means of a porte-lumière apparatus. The aquarium was 100 cm. long, 70 cm., wide and 50 cm. deep.

That light has a directly orienting effect on the animal is seen from the following experiment. The light was admitted through the slit, Fig. 1, *a*, and was reflected vertically downward upon the medusa, *b*, as it lay upon the bottom of the aquarium. The light fell upon one side of the medusa only, so that unilateral stimulation was produced. The cylinder of light was 5 cm. in diameter and therefore sufficient to cover one half of the body and the tentacles belonging thereto, even when extended. Owing to the difficulty of determining definitely the reaction when the medusa lay with its apex downward, it was in each case turned over. After one half of the bell had been illuminated for from 5 seconds to three minutes, the reaction occurred. The first movement carried the medusa vertically upward and it was only after it had pulsated three or four times that its path veered from the perpendicular. It might turn towards the light (Fig. 1, *bc*) or away from it (*bd*) or be so indefinite as not to be placed in either of these categories. The results of one hundred trials, upon different individuals in the main, are appended; those marked "indefinite" are the responses where the animal had not moved far enough to become oriented before ceasing to pulsate: —

Towards the light . . .	9 reactions.
Away from the light . . .	70 reactions.
Indefinite	21 reactions.

The effect of unilateral stimulation on a swimming jelly-fish

was tried. Care was taken to have the impinging ray as nearly as possible parallel to the oral-aboral axis of the animal. When thus illuminated, the medusa changed its course, moving away from the axis of light so that the path formed an acute angle with the ray.

Attention was then directed to the movements of Gonionemus when swimming freely in an aquarium illuminated from one direction. Figure 2 explains the arrangement. The sunlight was reflected through the aquarium from side to side (*xy*). A jelly-fish was freed at the point *a*, and it at once sank to the bottom. Within a few seconds it began to swim and finally reached the top of the water. The path, however, was not vertical, but was inclined away from the light as shown by the path *Ab*. On reaching the surface, the ordinary reaction took place whereby it inverted and sank in the vertical line *bB*. The process was repeated so that the resultant of the whole was the direction *Ah*. In this way it will be seen that the medusa ultimately reaches the farthermost point, as a result of the light acting exactly as in the simpler experiments in unilateral stimulation. In one case, that of a strong swimmer, the path followed was not broken by frequent inversions, inasmuch as the animal did not reach the surface until it had passed to the opposite side of the aquarium, a distance of about 70 cm.

That it is the direction of the ray of light that is the important factor in orientation, is made evident by the following experiment (Fig. 3). It will be seen that the light was thrown upon the aquarium at the angle indicated by the arrow, so that the end *abc*, lying nearer the source of light, is dark, the opposite end being illuminated. When a medusa starts at *b* in the light, it rises to the top and performs the actions just described, so that it reaches ultimately the end *d*. By this means we find an accumulation of jelly-fish in the end farthest from the light. Here they will remain until they die, or, as is often the case, they begin to swim regardless of the direction of the light and ultimately reach the shaded area, in which they settle down as described in my previous paper.

Yerkes [1] has described a very interesting response in Gonionemus

[1] Yerkes, R. M. Concerning the Behavior of Gonionemus. *Journ. Comp. Neur.*, 1906, vol. 16, p. 457–463.

under unilateral stimulation, a reaction observed many times by the writer. The animal is seen to pull the bell out of the light by means of its tentacles. Careful observation shows that the tentacles within the lighted area are not attached, but lie extended and passive. The bell itself is likewise motionless. The case is different with the portion of the bell and its tentacles lying in the shade, as these parts are generally more or less active. It is very improbable that there is any complex coordination here that

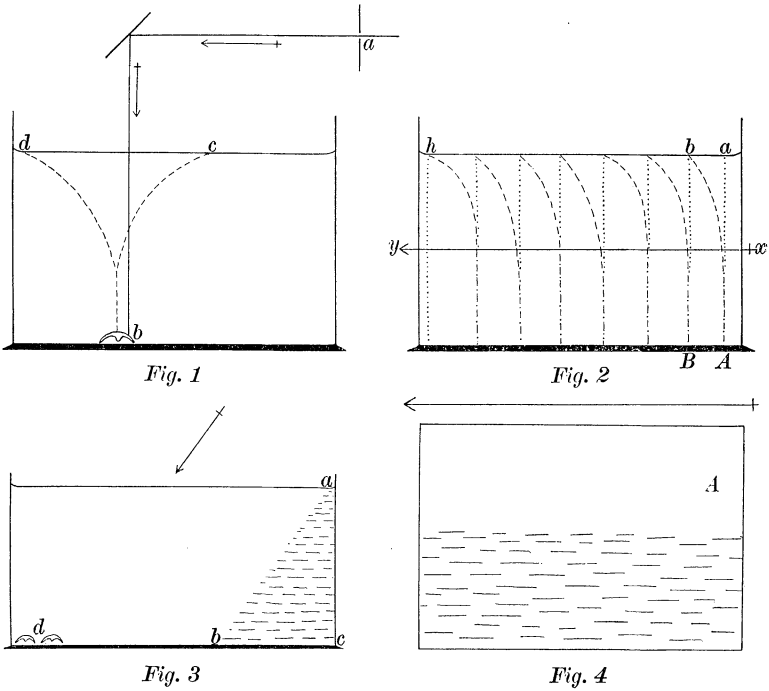

Fig. 1 *Fig. 2* *Fig. 3* *Fig. 4*

Figs. 1–4.—Diagrams illustrating the response of Gonionemus to light.

serves to move the body away from an area of light. The action seems to be wholly undirected. This interpretation is strengthened by the fact that, in some cases, the body has been drawn directly into the sunlight by those tentacles belonging to the illuminated side, the tentacles themselves being shaded. At other times the tentacles of one side of the body were seen to be carried up over the bell and to become attached to the underlying sand on the opposite side of the jelly-fish, after which the animal turned a

complete somersault by means of the tentacles. At first this was observed in medusae resting in the sunlight; the action was likewise seen in animals in the shade so that it has nothing whatsoever to do with the effect of light.

In the notes previously published, the writer made an attempt to determine the cause of the peculiar behavior of the animal in inverting the bell on reaching the surface of the water. The medusa has no mechanism other than contact whereby it can turn the bell on a transverse axis and thus invert it; it is never observed to turn in its path abruptly. As the equilibrium of the bell is destroyed when the animal reaches the surface and pushes one edge of the bell through the surface film, the inversion occurs. It frequently happens that medusae are found that will not remain mouth down even when so placed by hand. Such individuals kept from inverting pulsate violently for long intervals and come to rest only when they are turned over.

In the paper just cited, the writer interpreted the accumulation of Gonionemus in the shade as the result of trial and error. Further work has strengthened this conclusion. Only in the special case where the shadow will be met as the medusa moves away from the source of light, can this be *directly* the result of the orienting factor of light. This is shown in the experiment illustrated by Fig. 4, a view of the aquarium from above. The light is sent lengthwise through the aquarium and parallel with its base. One side is shaded. Individuals freed at *A* in the sunlight, move in their characteristic way to the farther end of the aquarium. Some, moving irregularly, enter the shaded area and remain there. Ultimately, the great majority of the animals are found in this area as described in the previous paper.

Yerkes[1] has described the light reactions of this medusa in the following words,—

"Gonionemus always settles down in a shaded region,—in other words, it is negatively photokinetic or photopathic.

When a number of the medusæ are placed in a glass vessel before a window they usually collect in the darkest region of the vessel. A simple test of this was made by putting a number of the animals in a dish having a bottom

[1] Yerkes, R. M. A Contribution to the Physiology of the Nervous System of the Medusa *Gonionemus murbachii*. Part I. *Amer. Journ.* Phys., 1902, vol. 6, p. 446.

16 × 10 inches and a depth of 3½ inches, one-half of which was covered with a black cloth. By way of illustration, the results of one test were as follows: eight animals were put into the dish in the afternoon at four o'clock; within fifteen minutes all were in the light half of the vessel, and there they remained with some changes of position until nine o'clock in the evening. At seven o'clock the next morning only one was in the light region, and of the others several were attached to the sides and bottom of the dark region of the dish. Similar results were gotten with several lots.

Again, when Gonionemi in a glass collecting pail are disturbed by agitation of the water, they swim about rapidly and in a few minutes most of them are found on the more intensely illuminated side of the vessel. If, now, they are allowed to remain undisturbed for an hour, they will be found either equally distributed throughout the vessel or collected in the darker region.

There are here two questions to be answered. First, why do the animals at first come to the light? Secondly, why is it that they are later found in the shaded regions? The following statement of the relation of the motor reaction of Gonionemus to stimulation by light accounts for the facts. In ordinary daylight they are, *when swimming*, positively phototactic; in very weak light, on the contrary, they are not directed by the stimulus to any considerable degree, and therefore appear to be indifferent. They come to rest in an intensity of light which is below that necessary to direct their movements to any important extent and are therefore negatively photopathic."

In a later paper[2] he described, as follows, a new set of experiments which corroborate his earlier conclusions.

"Eleven medusæ were placed in a white earthenware dish. The dish was illuminated by direct sunlight. After a few seconds, one-half of the dish was covered with a piece of black card-board. Within a minute ten of the eleven medusæ were in the sunlit portion of the dish and there they remained for about two and one-half minutes, swimming about actively but without moving far in any direction. Then as quickly as they had gathered in the sunlit portion they moved to the shaded portion and in less than a minute, all but two were in the shade of the cardboard."

In my former paper (p. 452) I stated that, by the use of a large jar, "33 cm. high and 21 cm. in diameter," no such reaction was observed. I can only add that the experiments conducted during the past summer with the aquarium 100 cm. by 70 cm. by 50 cm. bear out this conclusion. The collecting of the medusae in the light does not occur where large vessels are used and where reflections from the sides are eliminated. The writer believes that Yerkes' results were modified by the use of a small vessel with

[2] Yerkes, R. M. Concerning the Behavior of Gonionemus. *Journ. Comp. Neur.*, 1906, vol. 16, p. 459.

highly reflecting sides. Moreover, it is not clear from Yerkes' text that light of the same intensity was used since some of his experiments were conducted from 4 in the afternoon until 9 at night; at such times the light would be constantly decreasing in intensity. Again, he obtained the reaction by agitating the water, setting the medusae swimming in all directions. Under such conditions it would be very difficult to determine how much the movements of the jelly-fish were due to its own activities and how much to the currents set up by the agitation.

The writer's experiment described above where light was thrown on a swimming medusa shows too, that the reaction to light is the same in an individual swimming as in one at rest, and not different, as Yerkes believes. Inasmuch as experiments conducted under more normal and more carefully arranged conditions do not exhibit the reaction, the writer believes that Gonionemus is *at no time* positively phototactic.

These experiments lead, moreover, to the conclusion that the reaction of Gonionemus to light is a tropic one, and that the accumulation of the animals in shaded areas is referable to the method of "trial and error."

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